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Development of a True Ovoviviparous Sea Star, *Asterina pseudoexigua pacifica* Hayashi

MIÉKO KOMATSU, YASUO T. KANO[1], AND CHITARU OGURO

Department of Biology, Faculty of Science, Toyama University, Toyama 930, and [1]Uozu Aquarium, Uozu, Toyama 937, Japan

Abstract. *Asterina pseudoexigua pacifica* is a true ovoviviparous asteroid in that its development and metamorphosis occur within the spatial hermaphroditic gonad. From the middle of June to the middle of July, the gonad contains numerous embryos and juveniles in various stages through metamorphosis. The opaque, greenish yellow mature ovum is 450 μm in diameter. Development is direct. Embryos develop through wrinkled blastula and gastrula stages into a pear-shaped brachiolaria with three arms. The general process is similar to that of asteroids having direct development. Newly metamorphosed juveniles are released from the gonopores. Peak release occurs in the middle of July. The maximum number of juveniles released from an adult is about 1300. The juvenile is 900 μm in diameter and has two pairs of tubefeet in each arm; the skeletal plates are well developed. The present results are compared with those of other true viviparous echinoderms.

Introduction

The specific name *vivipara* has often been given to species that are believed to be viviparous, and a number of echinoderm species bear this name. Hendler (1979) noted about 60 viviparous ophiuroids, and many holothuroids also have this mode of development. The term "viviparity," however, should be restricted to the case in which embryos develop within the gonad or the genital tract, a portion of which may be specialized for incubating embryos. Coelomic or bursal incubation is a specialized type of brooding. If we accept this definition, only five species of echinoderms are known to be viviparous: Ophiuroidea, *Ophionotus hexactis* (by Mortensen, 1921), Holothuroidea, *Leptosynapta clarki* (by Everingham, 1961; cited from McEuen, 1987) and *Taeniogyrus contortus* (by Boolootian, 1966), Asteroidea, *Patiriella vivipara* (by Dartnall, 1969; Chia, 1976), and Concentricycloidea, *Xyloplax medusiformis* (by Rowe *et al.*, 1988). Descriptions of reproduction and development in these species, although sufficient to establish viviparity, are fragmentary.

Development through metamorphosis is known in about 40 of the 2500 extant asteroid species. Among these, reproduction and development are best known in several species of *Asterina*. The entire development through metamorphosis has been reported in *A. gibbosa* (Ludwig, 1882; MacBride, 1896), *A. coronata japonica* (Komatsu, 1975), *A. batheri* (Kano and Komatsu, 1978), and *A. minor* (Komatsu *et al.*, 1979). Larval development has been reported in *A. exigua*, *A. pectinifera*, and *A. regularis* (Mortensen, 1921; Komatsu, 1972). Sexuality and reproduction have been reported in some asterinid species (Cuénot, 1898; Ohshima, 1929; Bacci, 1949; Cognetti, 1954; Delavault, 1966; Dartnall, 1970; Emson and Crump, 1979; Komatsu *et al.*, 1979). Some species have direct development (yolky eggs and development only through the brachiolaria stage), while others have indirect development (non-yolky eggs and development through both the bipinnaria and brachiolaria stages). As to the sexuality of asterinids, some are gonochoric and some are hermaphroditic. Among the latter are *A. batheri*, *A. gibbosa*, *A. minor*, *A. pancerii*, *A. phylactica*, and *A. scobinata*. *Asterina minor* shows a breeding assemblage (Komatsu *et al.*, 1979). Thus, the diversity of development and reproduction occurring in various species belonging to the genus *Asterina* is well documented.

Asterina pseudoexigua pacifica was described by Hayashi (1977) as a new subspecies of *A. pseudoexigua* Dartnall. This subspecies differs from *A. pseudoexigua* in that its gonopores are on the abactinal side, and it is ovoviviparous. Development through metamorphosis takes

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Table I

Number and size distribution of juveniles of* Asterina pseudoxigua pacifica *collected in the field*

Number of tube-feet in the longest arm (in pairs)	Individual Number											
					April			May		June		
	July 30, 31 1974	Sept. 11, 12 1973	Dec. 7, 8 1972	Feb. 16 1976	23 1986	25 1975	28 1976	1, 2 1985	14, 15 1973	13 1976	21–25 1987	27–30 1986
2	37											
3	4	1		1		3	1				2	
4		9		5	6	6	3	2			13	1
5		9		20	8	7	11	14	4	2	29	7
6		4		34	16	8	26	45	1	6	58	22
7		1	2	16	15		28	56	2	11	32	34
8		1	8	4	5	1	11	30	1	19	36	21
9			12	2	1		1	10			32	9

* Juveniles bear fewer than nine pairs of tube-feet on the longest arm.

place in the gonad, and juveniles are released from the adult. The present report describes ovoviviparity and the entire process of development of *A. pseudoexigua pacifica.*

Materials and Methods

From time to time, between 1974 and 1987, specimens of *Asterina pseudoexigua pacifica* Hayashi were collected from the undersurface of stones in the intertidal zone of Kushimoto, Wakayama Prefecture (Fig. 1A). The number and size distribution of the juveniles collected are given in Table I. The specimens were kept alive in the laboratory.

Adults were cultured individually in small glass jars so that the release of embryos could be observed. During culture, the temperature was maintained similar to that of the natural habitat (20–25°C).

Embryos of various stages of development were obtained by dissecting the gonad at appropriate intervals between the middle of June to the middle of July.

General observations were made using dissecting and light microscopes. Living embryos were measured with an ocular micrometer. For microscopic examination of the skeletal system, juveniles were fixed in 70% alcohol, then macerated in a 10% aqueous solution of potassium hydroxide. For histological observations of the gonad, some specimens were fixed with Bouin's solution immediately after collection. The fixed material was embedded in paraffin, serially sectioned at 6 μm, and stained with Delafield's hematoxylin and eosin.

Gonads and embryos obtained from the gonad by dissection were fixed for scanning electron microscopy in 2% OsO_4 in 50 mM Na-cacodylate buffer (pH 7.4); the osmolarity of the fixative was adjusted by the addition of sucrose (final concentration, 0.6 M). The fixed materials were dehydrated in ethanol, dried with a critical-point dryer (Hitachi, HCP-2), and observed with a scanning electron microscope (Hitachi, S-510) after being coated with gold-palladium (Hitachi, E101 Ion Sputter).

Results

Ovoviviparity

The gonad is composed of clusters of lobules arranged in pairs in each interradius. Each gonad opens on the aboral side of the disk through a gonoduct (Fig. 1B). In early June, each gonad consists of ovarian and testicular portions (Fig. 1C, D). The majority of the eggs in the ovarian part are fully grown, nearly spherical (about 400 μm in diameter), and pale green. The head of the sperm contained in the testicular part is spherical (2–3 μm in diameter); the total length, including the tail, is 50 μm. This species is a spatial hermaphrodite, containing full-grown ova and active sperms simultaneously in each gonad.

The breeding season of *Asterina pseudoexigua pacifica* is from the middle of June to the middle of July, and most adults have many developing embryos or juveniles in their gonads. Developing embryos of particular stages can be obtained if the gonad is dissected at the appropriate time during the season: early cleavage and early gastrula stages in the middle of June (Fig. 2A, B); late gastrula stage from the middle to the end of June (Fig. 2C); brachiolariae from the end of June to the beginning of July (Figs. 1G, 2D and 2E); and metamorphosing larvae and juveniles from the beginning to the middle of July (Figs. 1H; 2F, G). There are some individual and yearly variations.

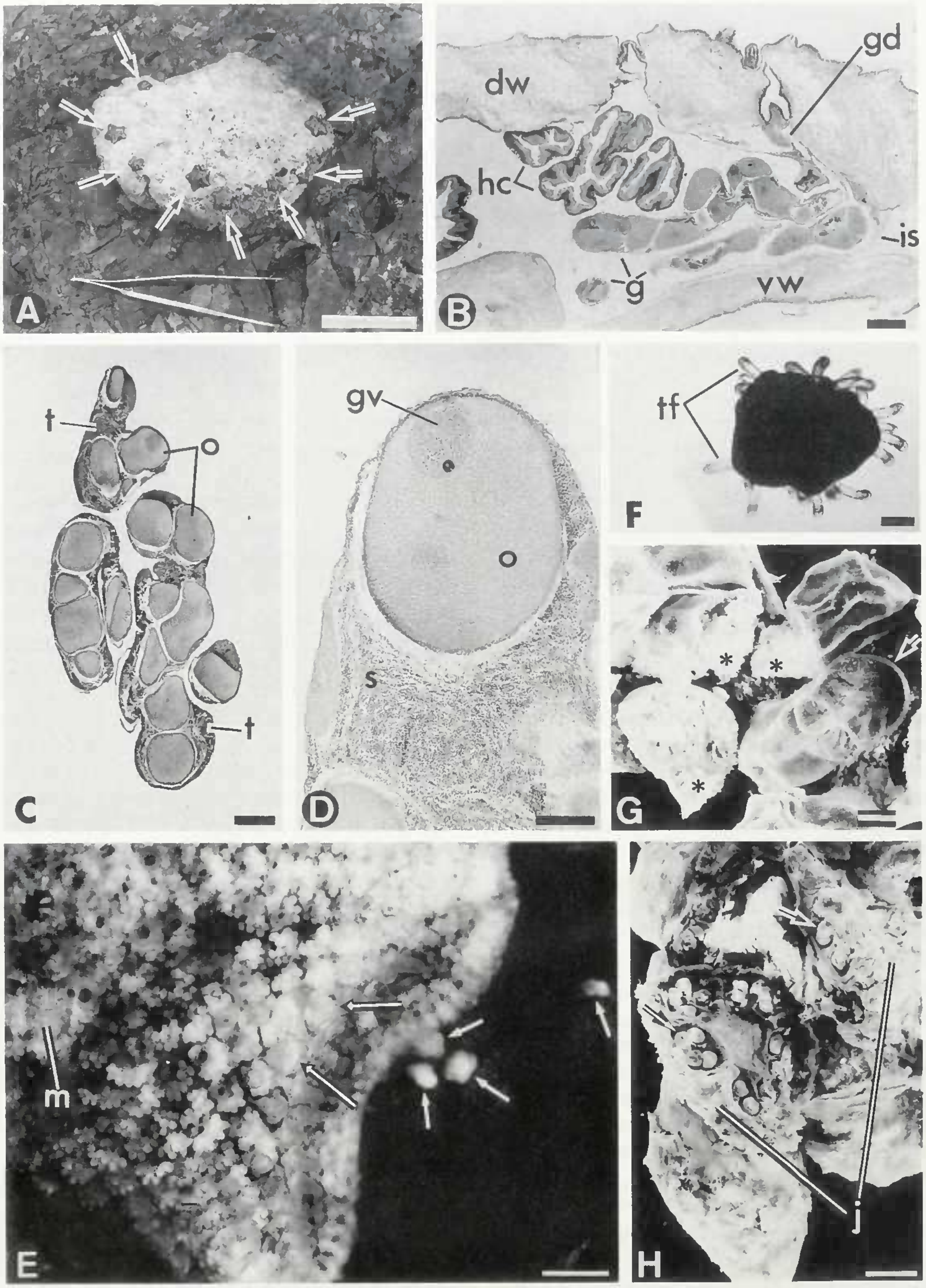

Figure 1. A. Specimens (arrows) of adult *Asterina pseudoexigua pacifica*, attached to the undersurface of a stone on the shore of Kushimoto. Bar scale = 50 mm. B. Sagittal section of the gonad (g) of *A. p. pacifica*. Note gonoduct (gd) passing through the dorsal wall (dw). Bar scale = 200 μm. hc, hepatic caecum; is, interradial septum; vw, ventral wall. C. Section of the hermaphroditic gonad of a specimen of *A. p. pacifica*. Note full grown ova and mature sperms. Bar scale = 200 μm. o, ovum; t, testicular portion. D. Magnified picture of the hermaphroditic gonad. Bar scale = 100 μm. gv, germinal vesicle; o, ovum; s, sperm.

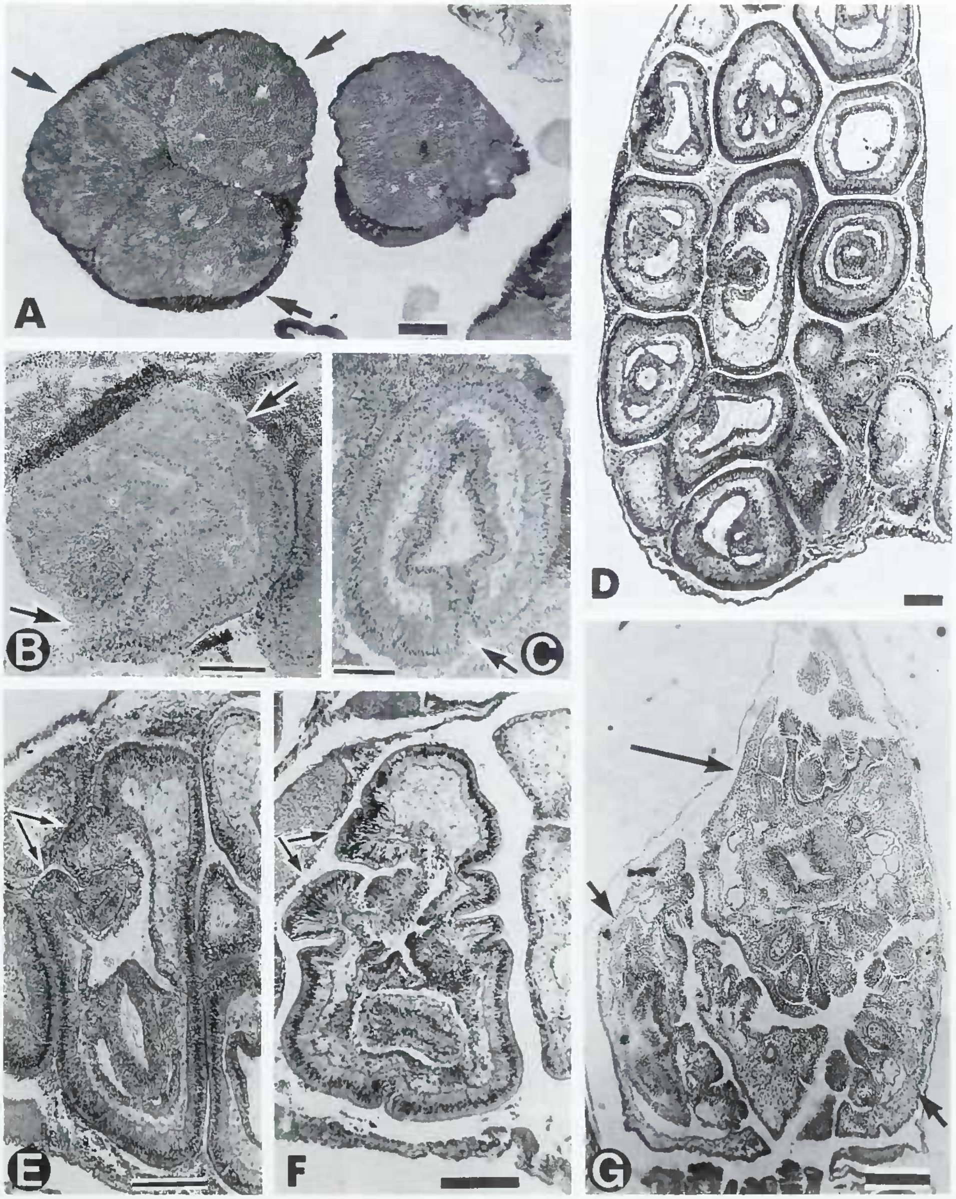

Figure 2. Micrographs of sections of the gonad of a specimen of *Asterina pseudoexigua pacifica*. Bar scale = 100 μm. A. Arrows point to three embryos in early cleavage. B. Wrinkled blastula with grooves (arrows). C. Sagittal section of a gastrula with a differentiated archenteron. Arrow indicates blastopore. D. Many embryos developing simultaneously in the gonad. E. Sagittal section of a brachiolaria with brachiolar arms (arrows). F. Sagittal section of a metamorphosing brachiolaria. Arrows show brachiolar arms. G. Horizontal (long arrow) and cross (short arrows) sections of juveniles in the gonad.

E. Dorsal view of a birthing specimen of *A. p. pacifica*. Short and long arrows indicate juveniles after birth and just appearing from gonopores, respectively. Bar scale = 1 mm. m, madreporite. F. Living specimen of a juvenile of *A. p. pacifica* just after birth, dorsal view. Bar scale = 200 μm. tf, tube-foot. G. Scanning electron micrograph of the inside of the gonad of a specimen of *A. p. pacifica*. Note brachiolaria (arrow) and metamorphosing larvae (asterisks). Bar scale = 100 μm. H. Same as Figure 1G, showing juveniles (j) with tube-feet (arrows) just prior to birth.

Development

Developing embryos of various stages are easily obtained by dissecting the gonads during mid-June to mid-July. The embryos usually fill the coelom of the adult. The developmental stages shown in Figures 3 and 4 represent embryos removed from dissected gonads; organogenesis (Fig. 2) was studied in sections of the gonad. Cleavage is total, equal, and radial (Fig. 4A). The early blastula is 450 μm in diameter and composed of equal-sized blastomeres (Fig. 4B). Figures 3C and 4C show blastulae in the most wrinkled stage. The surface of the blastula is divided by furrows into several portions, each consisting of clusters of blastomeres (Fig. 2B). Gastrulation takes place by invagination; the blastopore is circular and small (30 μm in diameter). Early gastrulae are 440 μm long and 380 μm wide. Hatching must follow the wrinkled blastula stage, because no fertilization membrane is ob-

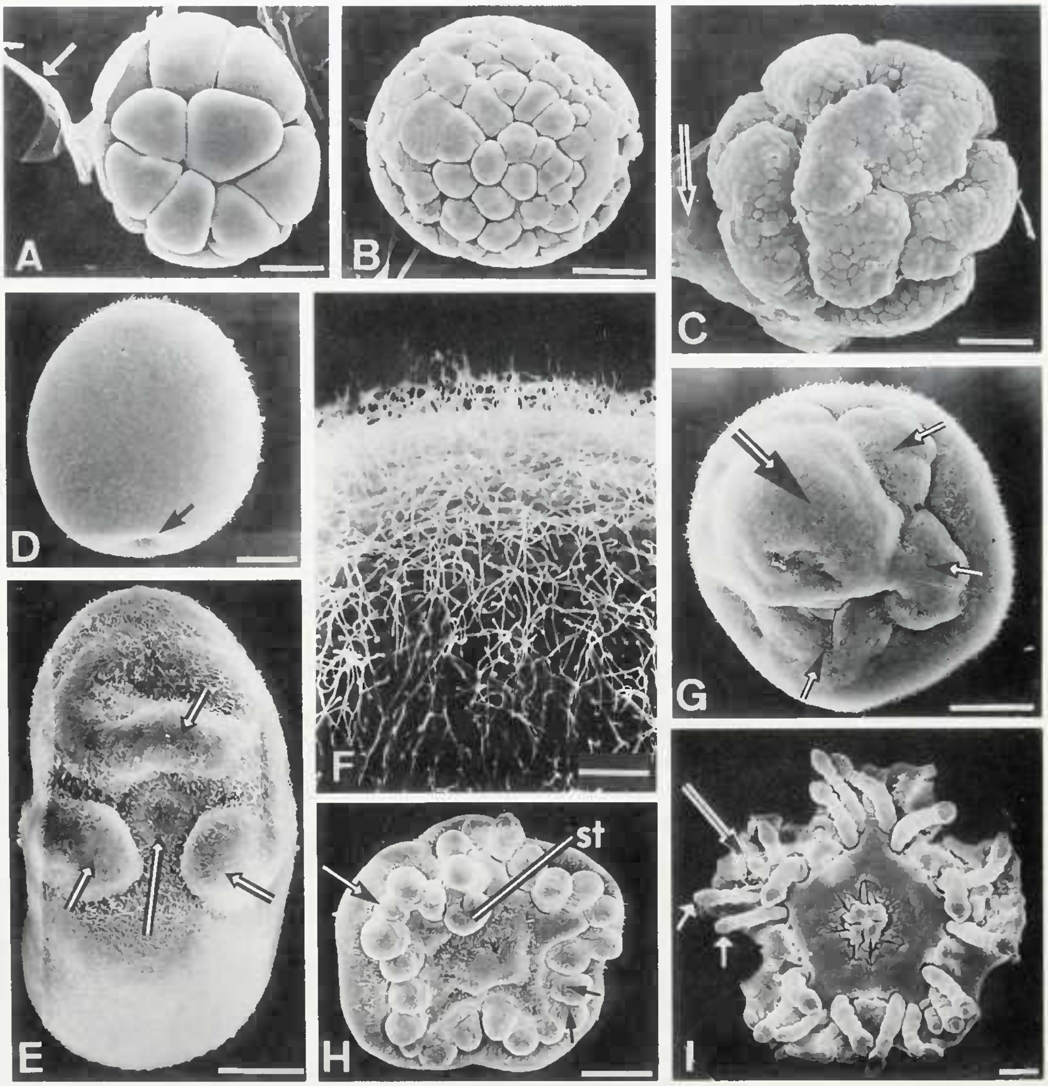

Figure 3. Scanning electron micrographs of specimens of *Asterina pseudoexigua pacifica*. The specimens shown in A–H were dissected out of the gonad. The juvenile shown in I was born from the gonopore. Bar scale = 100 μm. A. Embryo of an early cleavage with a fragment of the removed fertilization membrane (arrow). B. Early blastula. C. Wrinkled blastula in its most conspicuous stage. Arrow shows a fragment of the removed fertilization membrane. D. Early gastrula with blastopore (arrow) after hatching. E. Ventral side of a brachiolaria bearing three brachiolar arms (short arrows) and a central sucker (long arrow) among them. F. Magnified view of the anterior part of the specimen shown in Figure 3E, illustrating ciliation. G. Anterior view of the metamorphosing larva. Long and short arrows indicate stalk of larva and hydrolobes, respectively. Each hydrolobe has rudiments of a terminal tentacle and two pairs of tube-feet. H. More advanced metamorphosing larva with terminal tentacle (long arrow) and tube-feet (short arrows). st, stalk of larva. I. Juvenile after birth. Long and short arrows show a terminal tentacle and tube-feet, respectively.

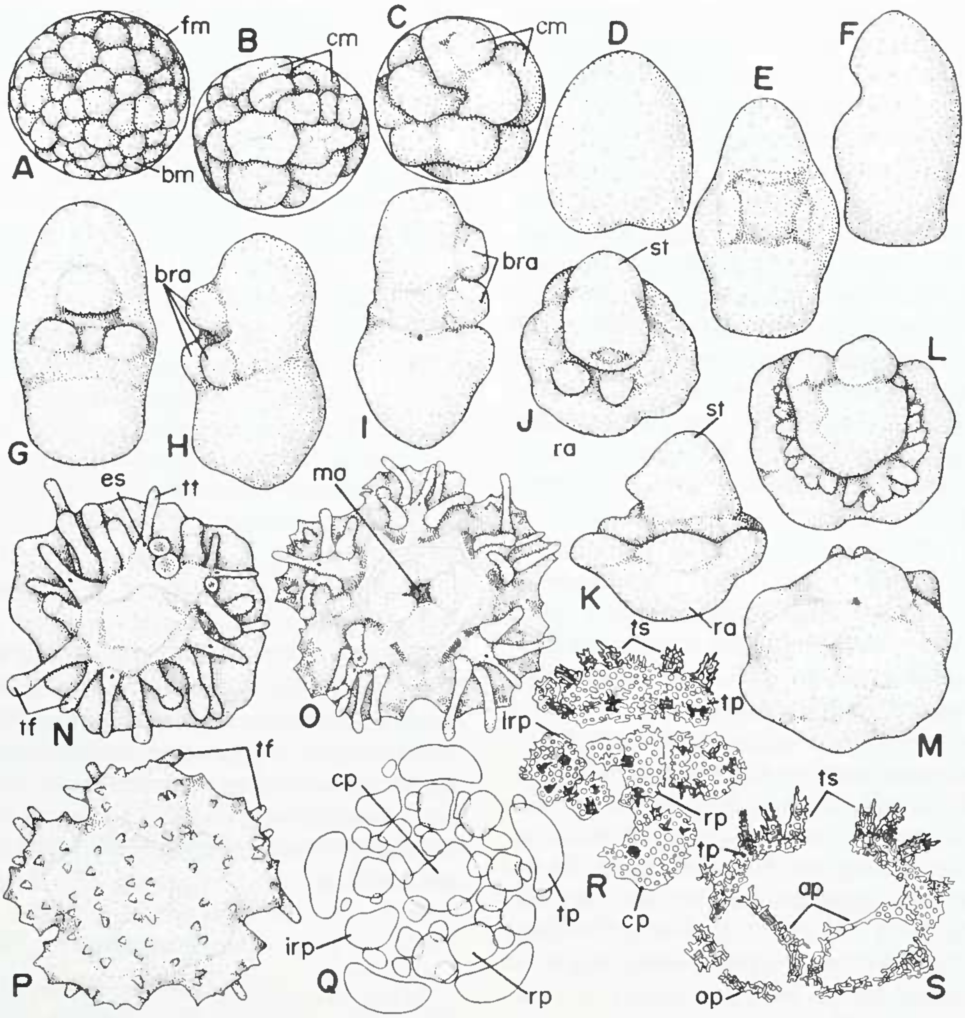

Figure 4. Development of *Asterina pseudoexigua pacifica.* Every drawing was made from a living specimen. Specimens in A–N and in O–S were either dissected out of the gonad, or born from the gonopores, respectively. A. Early blastula, earlier stage than that shown in Figure 3B. bm, blastomere; fm, fertilization membrane. B. Wrinkled blastula in earlier stage than that shown in Figure 3C. cm, cell mass. C. More advanced wrinkled blastula than that shown in Figure 3C. cm, cell mass. D. Early gastrula, same stage as shown in Figure 3D. E. Early brachiolaria, ventral view. F. Same as Figure 4E, left lateral view. G. Brachiolaria in earlier stage than that shown in Figures 3E and 4I. H. Same as Figure 4G, ventro-lateral (left) view. bra, brachiolar arm. I. More advanced brachiolaria, same stage as shown in Figure 3E, right lateral view. J. Metamorphosing larva in earlier stage than that shown in Figure 3G, anterior (future oral) view. st, stalk of larva. K. Same as Figure 4J, left lateral view. ra, rudiment of adult; st, stalk of larva. L. More advanced metamorphosing larva than that shown in Figure 3G, future oral view. M. Same as Figure 4L, future aboral view. N. Metamorphosing larva just before completion of metamorphosis, future oral view. es, eye-spot; tf, tube-foot; tt, terminal tentacle. O. Juvenile after birth, same stage as shown in Figure 3I, oral view. mo, mouth. P. Same as Figure 4O, aboral view. tf, tube-foot. Q. Schematic drawing of aboral skeletal system, same stage as shown Figure 4O. cp, central plate; irp, interradial plate; rp, radial plate; tp, terminal plate. R. Skeletal plates and spines of a ray of a specimen shown in Figure 4Q, aboral view. cp, central plate; irp, interradial plate; rp, radial plate; tp, terminal plate; ts, terminal spine. S. Same as Figure 4R, oral view. ap, ambulacral plate; op, oral plate; tp, terminal plate; ts, terminal spine.

served around the gastrula. Coelomic pouches emerge from the tip of the archenteron during the gastrula stage (Fig. 2C). Many mesenchyme cells are present in the blastocoel.

The larva of this sea star is a pear-shaped brachiolaria. Early brachiolariae with rudiments of brachiolar arms are shown in Figure 4E and F. Brachiolariae, which grow to become 600 μm long and 350 μm wide, bear three apparent brachiolar arms (Fig. 4G, H). Brachiolar arms are short; the lengths of the ventro-anterior arm and of the ventro-lateral arms are about 150 μm and 75 μm, respectively. At this stage, the blastopore is closed. Brachiolariae taken from the gonad can swim in seawater. The body surface of the larva is covered by cilia (Fig. 3E); they are about 10 μm long and are uniformly distributed at about 15/100 μm^2. Figures 2E, 3F, and 4I show more developed brachiolariae than those shown in Figure 4G and H. The posterior part of the larval body of this stage, which corresponds to the larval disk, becomes transformed into a subpentagonal form. A small hydropore is present near the center of the right side of the body. Three brachiolar arms become longer and project beyond the "central sucker," the triangular region defined by the bases of the three arms. The ventro-anterior arm is 175 μm long and ventro-lateral arms are 100 μm. The anterior part of the body, designated as the "stalk" of the larva, becomes translucent except for the tip of the brachiolar arms.

At metamorphosis, the stalk is absorbed (Fig. 2G). The posterior portion of the metamorphosing larva is hemispherical with a subpentagonal margin, being 450 μm in diameter. The metamorphosing larva, shown in Figure 4J and K, bears the shrunken stalk. The bulges of the hydrolobe become recognizable on the future oral side of the disk. Three brachiolar arms are still distinguishable at this stage. Tube-feet appear on the future oral side of the body in more advanced larvae (Fig. 4L, M). At this stage, the stalk is further reduced and situated in one interradius (Fig. 3H). The larva shown in Figure 4N has almost completed metamorphosis, and its diameter is 650 μm. The stalk has been completely absorbed. Two pairs of tube-feet and one terminal tentacle, which has a red eye-spot at the basal portion, are developed in each ray (Fig. 2G). When removed from the gonad, the larvae use their tube-feet to move on the substratum.

Release

Three adults, collected 4–7 July 1974 and kept individually in small jars, began to release juveniles from their gonopores on 10 July (individuals A, C, and I in Table II; Fig. 1F). Soon after release, the juveniles leave their mother and move around on the substratum with their tube-feet. The juveniles, about 900 μm in diameter, are white with a yellow tint (Figs. 1E; 4P, Q). They have two pairs of tube-feet in each arm, and their mouths are open. Skeletal plates (1 central, 5 interradial, and 5 radial plates on the aboral side; 5 pairs of oral and ambulacral plates on the oral side; and 5 terminal plates) are well developed (Fig. 4R, S, T). The release of juveniles by adults in the laboratory after mid-July has been observed since 1975. The number of juveniles released from adults is shown in Table II. The peak season of release is from 11 to 20 July. The maximum number of juveniles born from one adult was 1288.

Table II

Number of juveniles released from an adult of Asterina pseudoxigua pacifica

Individual	July 10	July 11–20	July 21–31	August 1–10	Total
A	20	1,179	82	7	1,288
B		996	4	15	1,015
C	3	957	1		961
D		263	3	32	298
E		257	1	2	260
F		158			158
G		113			113
H		63	17		80
I	3	50	16		69
J		46			46
K		28	5	9	42
L			17	22	39
M		35			35
N		6	9		15

Most juveniles collected at the end of July 1974 (Table I) had two pairs of tube-feet on each arm, so they had been born less than one month previously. In September and February, the juveniles collected from the field are on average larger than those collected in July. We conclude from these data that juveniles have more than five pairs of tube-feet (some with 6 or 7 pairs) in each arm one year after birth.

Discussion

Many echinoderms have been described as viviparous. These include 2 species of crinoids, 7 of holothuroids, and 70 of ophiuroids. *Isometra vivipara,* a crinoid, broods its eggs in a chamber, formed by pinnules, called a marsupium (Andersson, 1904; Mortensen, 1920). *Chiridota rotifera,* a holothuroid, broods its eggs in the coelom (Clark, 1910; Boolootian, 1966). *Stegophiura sculpta,* an ophiuroid, broods its larvae in the bursa (Murakami, 1941). But none of these species is truly viviparous, because development proceeds outside of the ovary or the genital tract.

Mortensen (1921) reported that development in *Ophionotus hexactis* begins in the ovary and, indeed, that the embryos develop entirely within the ovary. Everingham (1961; cited from McEuen, 1987) observed that *Leptosynapta clarki* is an intraovarian brooder. *Taeniogyrus contortus* was listed by Boolootian (1966) as a presumptive ovarian incubator. Dartnall (1969) reported that in *Patiriella vivipara* the embryonic development occurs in a sac derived from the gonad. However, he later noted that this species is a coelomic incubator (Dartnall, 1971). Although there is some discrepancy about the portion of the incubation (Dartnall, 1969, 1971), Chia (1976) reported that *P. vivipara* is an intraovarian brooder. Thus, *P. vivipara* seems to be a viviparous species. In *Xyloplax medusiformis*, development occurs in the ovary (Rowe *et al.*, 1988). Although this species is dioecious, eggs, sperms, embryos at various stages, and juveniles are present in the ovary. Thus, this species is truly ovoviviparous. Recently, Concentricycloidea, to which *X. medusiformis* belongs, has been regarded as a member of the subphylum Asterozoa, rather than of the Crinozoa or Echinozoa (Barker *et al.*, 1986). Therefore, further studies on the developmental process in *X. medusiformis* may provide important informations about true ovoviviparity in Asterozoa. Thus, previous descriptions suggest that the last mentioned five species are truly viviparous. The present study has shown that development of *Asterina pseudoexigua pacifica* commences and proceeds throughout metamorphosis within the gonad; the resulting juveniles are released from the gonopore. Thus, *A. pseudoexigua pacifica* is the sixth species of truly viviparous echinoderms.

Embryos of *A. pseudoexigua pacifica* have no tissue connection with the adult. Rather, the nutritional requirements of the embryos in these viviparous echinoderms seem to be supplied by nutrient reserves in the egg. Embryos of the bursal brooding ophiuroids, *Amphipholis japonica* and *Amphipholis squamata*, do have an organic connection with the bursal wall, and these ophiuroids were thought to be viviparous, the larva being brooded in the bursa and nourished by the adult (Murakami, 1940; Fell, 1946). But the tissue connection now appears to be a supporting structure, as had been suggested by Fell (1946).

Both male and female elements mature simultaneously in the gonads of *A. pseudoexigua pacifica*. Therefore, this species is spatially hermaphroditic. Spatial hermaphroditism has been reported in a few asterinid species: *Asterina gibbosa* (Cuénot, 1898; Bacci, 1949, 1951; Delavault, 1966), *Asterina minor* (Komatsu *et al.*, 1979) and *Asterina phylactica* (Emson and Crump, 1979), suggesting that spatial hermaphroditism is not rare in this genus.

Chia (1976) mentioned that *P. vivipara* is probably self-fertilizing. *Asterina minor* is self-fertilizing (Komatsu *et al.*, 1979). Fertilization in Echinodermata generally occurs in seawater, but Mortensen (1921) reported that ripe eggs of a true viviparous ophiuroid, *O. hexactis*, are fertilized in the ovary. Internal fertilization has not been described previously in any asteroid species. Although we have not observed natural self-fertilization in *A. pseudoexigua pacifica*, the development was initiated in the hermaphroditic gonads by injecting 1-methyladenine into the coelomic cavity of the adult in June. Therefore, we assume that self-fertilization takes place by the sperm of the same individual (Komatsu, unpubl.). The gonads of *A. pseudoexigua pacifica* have mature sperms and full-grown ova, simultaneously, in early June. The gonads contain many embryos or juveniles from mid-June to mid-July. These facts suggest that self-fertilization takes place internally.

Brooding occurs in many asteroid species, but the brooding habits differ with species (Feder and Christen, 1966; Hayashi, 1972). The protective location of the embryos varies: underneath the disk in *Leptasterias ochotensis similispinis* (Hayashi, 1943; Kubo, 1951); in a brooding chamber beneath the disk in *Henricia sanguinolenta* (Sars, 1844; Masterman, 1902), *Henricia tumida* (Hayashi, 1940), and *Leptasterias hexactis* (Osterud, 1918; Chia, 1966); in the nidamental chambers that are formed by interlocking spines at the arm bases in *Odinella nutrix* (Fisher, 1940); among the bases of the outspread spinelets of the dorsal paxillae in *Ctenodiscus australis* (Lieberkind, 1926); in the nidamental cavity between the aboral body wall and the supradorsal membrane in *Pteraster militaris* (Koren and Danielssen, 1857) and *Pteraster obscurus* (D'yakonov, 1968); and in the stomach in *Leptasterias grœnlandeca* (Lieberkind, 1920; Fisher, 1930).

Ovoviviparity may be considered to be a type of brooding. However, a definite difference exists between the viviparity and brooding outside the gonad. In asteroids, maturation of ova takes place during their release from the gonads. On the other hand, ova of the viviparous asteroid should mature within the gonads. Furthermore, many physiological changes must have occurred in the embryos during the change in adaptation, from the seawater environment, to the intraovarian circumstances. Viviparity is thus a very unique and specialized way of protecting the embryos in asteroids.

As adaptations for protecting offspring, specific methods and sites have been developed in each species during evolution. The ovoviviparity of *A. pseudoexigua pacifica* should reflect a period of evolution unsuitable for free larval life, during which the present species evolved.

Observations on the development of truly viviparous echinoderms are limited. Even in *O. hexactis*, the development of which has been thoroughly reported, the process of metamorphosis is unknown (Mortensen, 1921). Thus, the entire process of development of a true viviparous species is reported for the first time in the present study. Eggs of *A. pseudoexigua pacifica* are 450 μm in diameter, more than twice the size of those of *P. vivipara* (Chia, 1976; 150 μm) or of *O. hexactis* (Mortensen, 1921; 200 μm). *Patiriella vivipara* has no larval stage. Development of *X. medusiformis* is direct, and embryos are present in the gonad (Rowe *et al.*, 1988). In *L. clarki*, egg diameters range from 240 to 404 μm, and development proceeds, within the ovary, to tentacled juveniles through pentactula larvae (Everingham, 1961; cited from McEuen, 1987). *Ophionotus hexactis* has an ophiopluteus larva that is rudimentary, because the arms develop poorly and the anus is not open. The larva of *A. pseudoexigua pacifica* is a pear-shaped brachiolaria, similar to that of asteroids with direct development. Differences in the egg and the mode of development in these viviparous echinoderm species may indicate that ovoviviparity in echinoderms is a result of convergence.

Development of *A. pseudoexigua pacifica* is direct, with only a brachiolaria stage and without a bipinnaria. Direct development has been reported in other *Asterina* species: *A. batheri, A. burtoni, A. coronata japonica, A. exigua, A. gibbosa,* and *A. minor* (MacBride, 1896; Mortensen, 1921; James, 1972; Komatsu, 1975; Kano and Komatsu, 1978; Komatsu *et al.*, 1979). The eggs of these asterinids are yolky and large in diameter. The morphology of the larva of *A. pseudoexigua pacifica* resembles that of other asterinid species having direct development, especially *A. coronata japonica*. Brachiolariae of *A. pseudoexigua pacifica* and *A. coronata japonica* have short brachiolar arms and a poorly developed central sucker. All asterinids undergoing direct development have a pelagic larval phase, except for *A. exigua, A. gibbosa,* and *A. minor*. Although the larvae of *A. pseudoexigua pacifica* remain in the gonad throughout their development, they have cilia on the body surface and can swim in seawater when removed from the ovary. Furthermore, the larvae continue developing in seawater (Komatsu, unpubl.). Hence, the larva of the ancestor of *A. pseudoexigua pacifica* may have been free-swimming in seawater like the larvae of some other asterinids. Although *A. pseudoexigua pacifica* is ovoviviparous, it has the same developmental type, egg, and brachiolaria as other non-viviparous asteroids. This suggests that ovoviviparity in *A. pseudoexigua pacifica* evolved recently from the direct type with free-swimming brachiolaria.

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